

1 **Positive work contribution shifts from distal to proximal joints during a prolonged run**

2

3

4 Maximilian Sanno^{1,2}, Steffen Willwacher^{1,3}, Gaspar Epro^{1,4} and Gert-Peter Brüggemann^{1,2,3}

5

6 ¹ Institute of Biomechanics and Orthopedics, German Sport University Cologne, Cologne,

7 Germany

8 ² German Research Center of Elite Sport, German Sport University Cologne, Cologne,

9 Germany

10 ³ Institute of Functional Diagnostics, Cologne, Germany

11 ⁴ Sport and Exercise Science Research Center, School of Applied Sciences, London South

12 Bank University, United Kingdom

13

14

15 Address for correspondence:

16 Maximilian Sanno

17 Institute of Biomechanics and Orthopedics

18 German Sport University Cologne

19 Am Sportpark Müngersdorf 6

20 50933 Cologne, Germany

21 Tel.: +49-221-49827630

22 Fax: +49-221-4971598

23 Email: m.sanno@dshs-koeln.de

24

25 **ABSTRACT**

26 **Purpose:** To investigate the joint-specific contributions to the total lower extremity joint work
27 during a prolonged fatiguing run. **Methods:** Recreational long-distance runners (RR; n = 13)
28 and competitive long-distance runners (CR; n = 12) performed a 10-km treadmill run with near-
29 maximal effort. A three-dimensional motion capture system synchronized with a force-
30 instrumented treadmill was used to calculate joint kinetics and kinematics of the lower
31 extremity in the sagittal plane during the stance phase at 13 distance points over the 10-km run.
32 **Results:** A significant ($P < 0.05$) decrease of positive ankle joint work as well as an increase
33 of positive knee and hip joint work was found. These findings were associated with a
34 redistribution of the individual contributions to total lower extremity work away from the ankle
35 towards the knee and hip joint which was more distinctive in the RR group than in the CR
36 group. This redistribution was accomplished by significant ($P < 0.05$) reductions of the external
37 ground-reaction force (GRF) lever arm and joint torque at the ankle and by the significant (P
38 < 0.05) increase of the external GRF lever arm and joint torque at the knee and hip.
39 **Conclusion:** The redistribution of joint work from the ankle to more proximal joints might be
40 a biomechanical mechanism that could partly explain the decreased running economy in a
41 prolonged fatiguing run. This might be because muscle-tendon units crossing proximal joints
42 are less equipped for energy storage and return compared to ankle plantar flexors and require
43 greater muscle volume activation for a given force. In order to improve running performance,
44 long-distance runners may benefit from an exercise-induced enhancement of ankle plantar
45 flexor muscle-tendon unit capacities.

46 **Key Words:** LOCOMOTION, RUNNING MECHANICS, JOINT TORQUE, ANKLE
47 JOINT, LEVER ARM, RUNNING ECONOMY

48 INTRODUCTION

49 Long-distance running is one of the most popular recreational activities in the world and is
50 often performed with competitive effort. High-performance runners differ from less successful
51 ones mainly in terms of the energy demand for a given submaximal running velocity, with
52 lower steady-state oxygen uptake indicating better running economy (1). Running economy is
53 a useful predictor of endurance running performance, which depends on a complex interplay
54 of factors such as the runner's training level, environment, anthropometric parameters,
55 physiology, and biomechanics (1). From a biomechanical perspective, running economy can
56 be related to spatio-temporal running characteristics (2), kinetics of the center of mass (CoM),
57 joint kinematics, and the tendons' capacity to store and return elastic energy (1,3,4). However,
58 no biomechanical parameter alone can explain the complexity of human running economy
59 (2,5).

60 Severe modifications of the running style, such as exaggerated knee flexion during the
61 stance phase (i.e., Groucho running), substantially reduce running economy by increasing
62 oxygen uptake (6). Reduction of running economy also occurs during sustained long-distance
63 runs performed until exhaustion (7,8). Fatigue, defined as exercise-induced reduction in the
64 ability to generate muscle force or power due to changes in the neural drive or exhaustion of
65 contractile function (9), can cause a decline in running velocity and changes in spatio-temporal
66 running characteristics and spring-mass behavior (10). However, whether these changes occur
67 when the running velocity is kept constant (as for instance during running on a treadmill) is
68 currently not clear (11–14). Furthermore, despite one study indicating that knee flexion angle
69 at foot contact and mid-stance may be more flexed due to exhaustion on a treadmill (15), most
70 reports show relatively constant hip, knee, and ankle joint kinematics during prolonged
71 fatiguing treadmill runs (13,16). This appears to be independent of the performance level of

72 runners performing a 10-km treadmill run to volitional exhaustion at a velocity approximating
73 their 10-km race pace (17).

74 Only a few studies have examined the effects of exhaustion on running kinetics during
75 constant-velocity runs. In general, vertical ground-reaction force (GRF) and leg stiffness
76 decrease during exhausting running, whereas vertical stiffness tends to be rather constant
77 (11,14,18,19). However, considerable inter-individual differences seem to exist in the fatigue-
78 induced changes in running kinetics (18,19). It is surprising that most reports investigating
79 exhausting running have focused on CoM kinetics, although it is known that CoM work is the
80 result of a complex interaction of the joint work done by individual muscles, especially at the
81 lower extremity (20,21). A joint-specific view allows to describe the individual contributions
82 of different muscle groups to the total work of the lower extremity (22–24).

83 Negative work is facilitated by forcefully stretching activated muscle fascicles or
84 passive elastic structures within the muscle-tendon unit. Positive work originates from active
85 shortening of muscle fascicles or the return of potential strain energy previously stored within
86 passive elastic structures (25,26). Among the different muscle groups of the lower extremity,
87 the ankle plantar flexors are one of the main contributors to total joint work of the lower
88 extremity during running (20–22). It is notable that the relative contribution of ankle plantar
89 flexors does not seem to alter, even when the running velocity is changed (20–22). However,
90 other observations have identified an age-related proximal shift of the individual joint
91 contributions in walking and running in older adults. This is represented foremost by a reduced
92 ankle joint contribution which seems to be due to a reduced ankle plantar flexor muscle strength
93 compared to other more proximal muscle groups (27–30). This indicates that changes in the
94 contractile properties of the lower extremity muscles may lead to modifications in the joint-
95 specific contribution during human locomotion, including running. The literature provides
96 indications towards an altered joint-specific contribution in response to running-induced

97 fatigue. For example, the maximal muscle strength of hip and knee extensors, and ankle plantar
98 flexors have been demonstrated to decrease after long-distance running, especially following
99 ultra-marathons (31–33). Specifically, running a half marathon, intensive treadmill running
100 over 2 hours or a 5-km run have shown to decrease the isometric ankle plantar flexor muscle
101 strength (34–36).

102 The triceps surae muscle (TS) is the main plantar flexor of the foot and consists of the
103 soleus and the biarticular gastrocnemius. The relatively short muscle fascicles and pennate
104 architecture of the TS (37,38) allow it to generate force at a lower metabolic cost than longer
105 fibered muscles such as the knee extensors (25). This facilitates an efficient energy storage and
106 return within the long Achilles tendon (26). Theoretically, greater energy storage and return
107 would reduce the work needed to be done by the muscle fascicles during the propulsion phase
108 in running and therefore improve running economy (39). This effect has been confirmed in a
109 study that demonstrated that an increase of the ankle plantar flexor muscle strength by
110 resistance training could reduce oxygen uptake and thus increase running economy (3).
111 Furthermore, well-trained distance runners with a good running economy show greater ankle
112 plantar flexor muscle strength and greater tendon-aponeurosis stiffness than runners with lower
113 running economy (4).

114 Although it is known that there are differences in individual joint contributions during
115 running, no studies have investigated if and how joint-specific work is altered over the course
116 of a prolonged fatiguing run (especially when performed at constant velocity) and whether
117 there are differences between recreational and competitive runners. The current study therefore
118 aimed to investigate the joint-specific contributions to the total lower extremity joint work
119 during a prolonged fatiguing run in recreational and competitive long-distance runners. The
120 primary hypothesis was that a long-distance run with near-maximal effort would change the
121 work contributions of the lower extremity joints, characterized by a reduction of work at the

122 ankle joint. A secondary hypothesis was that recreational runners would experience greater
123 running-induced reduction of ankle joint work than competitive long-distance runners. The
124 results of the present study might improve our understanding of fatigue-related alterations in
125 running mechanics and reductions in running economy in prolonged fatiguing runs.

126 **METHODS**

127 **Participants**

128 A total of 25 male runners were recruited and separated into two groups based on their
129 individual long-distance running performance level. The recreational runners (RR) group
130 included physically active students ($n = 13$; age 24.3 ± 3.4 years; height 1.84 ± 0.05 m; mass
131 81.3 ± 7.4 kg) with individual season best times $>47:30$ min in a 10-km run. The competitive
132 runners (CR) group included competitive long-distance runners ($n = 12$; age 24.7 ± 3.8 years;
133 height 1.82 ± 0.06 m; mass 73.0 ± 7.9 kg) with individual season best times $<37:30$ min in a
134 10-km run. Runners with self-reported history of musculoskeletal injury of the lower extremity
135 in the preceding 12 months were excluded. Each participant signed a written informed consent
136 prior to the study. The Research Ethics Committee of the German Sport University Cologne
137 approved this study (No. 102/2017). All procedures were in accordance with the Declaration
138 of Helsinki.

139 **Experimental protocol**

140 All participants performed a 10-km treadmill run with near-maximal effort (105% of their
141 individual season best time over the 10-km distance). The near-maximal effort was selected for
142 safety reasons and to ensure that all participants could complete the task. The average
143 calculated 105% time was $52:49 \pm 2:21$ min (approximate running velocity of $3.2 \text{ m}\cdot\text{s}^{-1}$) for
144 the RR group and $37:32 \pm 1:17$ min (approximate running velocity of $4.4 \text{ m}\cdot\text{s}^{-1}$) for the CR
145 group. The treadmill's inclination was set at 0% to avoid the effects of gradient on running
146 kinematics or kinetics. All participants wore light-weight (~ 0.170 kg) racing flat shoes

147 (Adizero Pro 4; Adidas AG, Herzogenaurach, Germany). A practice run was performed 7 days
148 before the actual run to allow participants to familiarize with the racing flat shoe and the
149 treadmill. All participants stated that they regularly used different kinds of running shoes,
150 including racing flat shoes. No further footwear adaptation was conducted. Prior to the
151 treadmill run, the participants performed warm-up exercises with self-determined duration.
152 During the actual treadmill run the participants were continuously encouraged and kept
153 informed of the covered distance.

154 **Monitoring of heart rate and rating of perceived exertion**

155 A heart rate monitor (M51; Polar Electro, Kempele, Finland) kept track of the heart rate during
156 the run to quantify the cardiovascular load. Immediately after the run, the Borg scale was used
157 for rating perceived exertion (on a scale of 6–20).

158 **Kinematics and kinetics**

159 The kinematics and kinetics were captured with 13 infrared cameras using a three-dimensional
160 motion capture system (250 Hz, MX-F40; Vicon Motion Systems, Oxford, UK) synchronized
161 with four multi-axis force transducers (1000 Hz, MC3A-3-500-4876; AMTI Inc., Watertown,
162 USA) embedded in a single-belt treadmill (Treadmetrix, Park City, USA). Prior to motion
163 capturing, spherical retroreflective markers (diameter: 13 mm; ILUMARK GmbH,
164 Feldkirchen/Munich, Germany) were attached to 78 bony landmarks (40). The markers for the
165 foot were attached at the corresponding positions on the shoe. All marker trajectories and the
166 GRF data were smoothed using a recursive, fourth-order digital Butterworth filter with a cutoff
167 frequency of 20 Hz.

168 A three-dimensional inverse dynamics model of the total body, consisting of 15 rigid
169 body segments (40, 41), was implemented to calculate the kinematic and kinetic parameters of
170 the CoM and lower extremity, using custom MATLAB routines (MathWorks Inc., Natick,
171 USA). Body height and body mass were imported to the model to obtain the inertial properties

172 for each segment (40,42). Joint torques were expressed in the anatomical coordinate system of
173 the proximal segment. External GRF lever arms were determined within the sagittal plane and
174 expressed in the coordinate system of the proximal segment. Lever arms were obtained by
175 dividing the GRF term of Hof's explicit joint torque equation (41) by the amplitude of the GRF
176 vector. A reference trial was recorded in an upright position to determine the neutral position
177 of all joints (0° joint angle) prior to the beginning of the run. The hip joint center was
178 determined using the regression equations provided by Bell and co-workers (43). The negative
179 and positive work at the hip, knee, and ankle joint was calculated over the entire stance phase
180 by numerical integration of the power-time curve. Positive work was determined by summing
181 up all positive integrals and negative work by summing up all negative integrals during the
182 entire stance phase (21).

183 **Parameters**

184 Step length, step frequency, and contact time were assessed for spatio-temporal
185 characterization of the running. Additionally, various kinematic and kinetic parameters were
186 determined during the stance phase of the right leg from the sagittal plane for further analysis
187 over the course of the run. To improve reliability, the data were averaged over 20 stance phases
188 at each of the 13 distance points (0 km, 0.2 km, 0.5 km, 1 km, 2 km, 3 km, 4 km, 5 km, 6 km,
189 7 km, 8 km, 9 km, and 10 km). Positive and negative work were calculated for the hip, knee,
190 and ankle joint. Subsequently, the relative joint-specific contributions to the total lower
191 extremity joint work were determined. Further, joint kinetic (maximal power and maximal
192 external torque) and joint kinematic (maximal angular velocity and angle) parameters were also
193 assessed. External GRF lever arms of all three joints were determined at the instant of maximal
194 vertical GRF. All kinetic parameters were normalized to total body mass. To describe the
195 vertical displacement of the total body, the CoM height at touch-down of the foot (CoM_{TD}),
196 and at the minimal height (CoM_{min}) during the stance phase were calculated.

197 **Statistical analysis**

198 Two-way repeated-measure analysis of variance (ANOVA) with performance level (RR vs.
199 CR) as between subject factor was used to analyze the effects of running distance at all 13
200 distance points. If a significant running distance main effect or interaction effect between
201 performance level and running distance was detected by two-way ANOVA, a univariate
202 repeated-measures ANOVA with 78 pairwise post-hoc comparisons using Bonferroni
203 correction (resulting in an adjusted alpha level of 0.000641) was applied for each group to
204 determine any significant differences between the various distance points. The values obtained
205 at the different distance points were compared with the values at the beginning of the run (0
206 km). All parameters were presented as group means (and standard deviations). Cohen's *d* effect
207 sizes were calculated to explain the strength of an observed effect, using the equation

208
$$d = \frac{\bar{x}_j - \bar{x}_i}{\sqrt{\frac{s_j^2 + s_i^2}{2}}}$$

209 with $\bar{x}_{i,j}$ as the average and $s_{i,j}^2$ as the sample variance of different distance points. The
210 subscript *i* represented the 0 km distance point. The subscript *j* represented the different
211 distance points after the 0 km distance point (0.2 km to 10 km). Effect sizes of ≥ 0.2 were
212 considered as small, ≥ 0.5 as medium, and ≥ 0.8 as large (44). The partial eta squared (η_p^2) value
213 was determined to explain the proportion of the total variance between both groups, the running
214 distance main effect, and the interaction effect between performance level and running
215 distance, respectively. Cohen (44) suggested norms for η_p^2 as small (0.01), medium (0.06), and
216 large (0.14). Significance for all statistical procedures was tested at a level of $\alpha = 5\%$ ($P < 0.05$)
217 using SPSS Statistics 23 (IBM Corp., Armonk, NY, USA).

218 **RESULTS**

219 Perceived exertion after the run was comparable between the two groups (RR: 16.9 ± 1.3 ; CR:
220 17.1 ± 1.2), although maximal heart rates were significantly different (RR: 171 ± 14 BPM; CR:

221 186 ± 10 BPM; $P = 0.023$, $\eta_p^2 = 0.206$) after the 10-km distance. There were significant ($P <$
222 0.05) differences between the groups in each of the analyzed spatio-temporal parameters,
223 which could be related to the different running velocity. However, none of the spatio-temporal
224 parameters changed significantly over the course of the run in either group. ~~For additional~~
225 ~~details, (see [Appendix, supplemental-Supplemental-digital-Digital content](#) Content 1 (SDC 1),)~~
226 Tab. 1 -- [Group means and standard deviations of heart rate and spatio-temporal parameters;](#)
227 [SDC 1, and Fig. 1 left top -- Changes in heart rate; SDC 1, Fig. 1 left center -- Changes in step](#)
228 [length; SDC 1, Fig. 1 right center -- Changes in step frequency; SDC 1, Fig. 1 central bottom](#)
229 [-- Changes in contact time\).](#)

230 **Joint work**

231 There was a significant ($P < 0.05$) running distance main effect for all positive and negative
232 joint works other than the negative ankle joint work. For the joint work, a significant ($P < 0.05$)
233 intergroup effect was found only for the negative ankle joint work, with the RR group showing
234 relatively lower negative hip, knee, and ankle joint work. ~~For additional details, (see [Appendix,](#)~~
235 [SDC 1, Tab. 1 -- Group means and standard deviations of joint work\).](#)

236 The positive joint work of the ankle decreased significantly ($P = 0.002$, $d = 0.88$) and
237 the positive joint work of the knee increased significantly ($P = 0.046$, $d = 0.69$) from the
238 beginning to the end of the run in the RR group (Fig. 1). In the RR group, the positive work of
239 the ankle joint decreased significantly for the first time at 5 km ($P = 0.017$) which continued to
240 decrease up to the end of the run whereas, in the CR group, positive work of the ankle joint
241 showed a steady modest decrease over the course of the run (Fig. 2). In the RR group, there
242 was a slight increase in the positive joint work at the knee and hip joint, with statistically
243 significant ($P < 0.05$) increase at the knee joint at 2 km, 8 km, and 10 km. The further distance
244 points between 2 km and 8 km as well as the 9 km were slightly above the level of significance
245 ($P > 0.05$). In the CR group, the positive work showed a minor increase at the knee joint, but

246 did not change at the hip joint (Fig. 2). A significant ($P < 0.05$) intergroup difference but no
247 running distance main effect was seen for the total positive work of all three joints (Tab. 1).
248 Therefore, it is not surprising that the relative joint-specific contributions to the total positive
249 lower extremity joint work showed changes from the beginning of the run (hip 19%, knee 29%,
250 ankle 52%) to the end of the run (23%, 33%, 44%) in the RR group but not in the CR group
251 (beginning of the run: hip 22%, knee 28%, ankle 50% vs. end of the run: 22%, 31%, 47%).

252 *** insert Figure 1 about here ***

253 In the RR group, negative joint work was slightly increased at the hip, knee, and ankle over the
254 course of the run. In contrast, the negative knee joint work of the CR group was only slightly
255 increased and at the ankle slightly decreased (Fig. 2). There was no running distance main
256 effect but a significant ($P < 0.001$) intergroup difference and a significant ($P = 0.015$)
257 interaction effect between performance level and running distance for the total negative work
258 of all three joints. The RR group showed a distinctly higher increase in total negative work of
259 the lower extremity than the CR group (+9% vs. -1%; Tab. 1). However, the relative joint-
260 specific contributions to the total negative lower extremity joint work remained unchanged in
261 both groups over the course of the run (RR group: hip 7%, knee 45%, ankle 48% at 0 km vs.
262 8%, 45%, 47% at 10 km; CR group: 7%, 34%, 59% at 0 km vs. 8%, 36%, 56% at 10 km).

263 *** insert Figure 2 about here ***

264 **Joint torque and external GRF lever arm**

265 A significant ($P < 0.05$) running distance main effect was identified for all joint torques, with
266 significant ($P < 0.05$) intergroup differences in the knee and ankle joint torques (Tab. 1). In the
267 RR group, hip joint torque showed a significant ($P < 0.05$) increase for the first time at 6 km
268 which continued to increase until the end of the run; in the CR group, hip joint torque showed
269 a slight nonsignificant increase over the course of the run. In both groups, knee torque increased
270 slightly and ankle torque decreased slightly over the course of the run (Tab. 1). Significant (P

271 < 0.05) running distance main effects were seen for the external GRF lever arm of all three
272 joints (Tab. 1). The external GRF lever arm of the ankle was slightly decreased, while the GRF
273 lever arm of the knee and hip joint was slightly increased (Fig. 3).

274 *** insert Table 1 about here ***

275 *** insert Figure 3 about here ***

276 **Joint angle and angular velocity**

277 We found a significant ($P < 0.05$) running distance main effect for the maximal knee flexion
278 angle and for the knee flexion angle at touch-down of the foot. The knee flexion angle at touch-
279 down of the foot increased significantly ($P < 0.05$) over the course of the run in both groups
280 (Tab. 2). Additionally, the RR group showed a significant ($P < 0.05$) increase in the maximal
281 knee flexion angle and a significant decrease in plantar flexion angle at toe-off over the course
282 of the run (Tab. 2). A significant ($P < 0.05$) intergroup difference in the ankle plantar flexion
283 angle at touch-down of the foot was observed which can explain the difference in foot
284 positioning at touch-down of the foot (Tab. 2). Maximal ankle dorsiflexion did not change.
285 Significant ($P < 0.05$) running distance main effects were seen for maximal knee extension
286 velocity and for maximal ankle plantar flexion velocity (Tab. 2). In the CR group, the maximal
287 ankle plantar flexion velocity showed a significant ($P < 0.05$) increase for the first time at 2 km
288 which continued to increase until the end of the run (Tab. 2).

289 **CoM kinematics and GRF**

290 Significant ($P < 0.05$) running distance main effects were found for CoM_{TD} and CoM_{min} . Both
291 parameters decreased significantly ($P < 0.05$) over the course of the run, especially in the RR
292 group (Tab. 2). Further results can be found in the Appendix For additional results of joint
293 kinetics, joint kinematics, CoM kinematics, and maximal vertical GRF, please (SDC 1, Tab. 1
294 -- Group means and standard deviations of joint kinetics, joint kinematics, CoM kinematics,
295 and the maximal vertical GRF; SDC 1, Fig. 1 right top -- Changes in vertical GRF; SDC 1, Fig.

296 2 -- Changes in external joint torques and hip flexion angle; SDC 1, Fig. 3 -- Changes in joint
297 angles; SDC 1, Fig. 4 -- Changes in angular velocities; SDC 1, Fig. 5 -- Changes in center of
298 mass heights; SDC 1, Fig. 6 -- Changes in joint power).~~refer to Tab. 1 and Fig. 1-6 of the SDC.~~

299 *** insert Table 2 about here ***

300 **DISCUSSION**

301 The purpose of this study was to investigate the joint-specific contributions to the total lower
302 extremity joint work during a prolonged fatiguing run in recreational and competitive long-
303 distance runners. The primary hypothesis of this study was that a long-distance run with near-
304 maximal effort would change the work contributions of the lower extremity joints,
305 characterized by a reduction of work at the ankle joint. The joint work magnitudes in the current
306 study are comparable with the findings of Roy et al. (24). We found a running distance main
307 effect on the positive and negative work at all three joints, except for negative work at the ankle
308 joint. The decrease in positive ankle joint work was counteracted by increases in positive knee
309 and hip joint work. Over the course of the 10-km treadmill run with near-maximal effort, joint-
310 specific contributions to positive work displayed a clear redistribution away from the ankle
311 towards the knee and hip joints. Therefore, our primary hypothesis can be accepted.

312 When trying to reveal the potential underlying mechanisms, we found that knee and hip
313 joint flexion angles slightly increased over the course of the 10-km treadmill run, but the ankle
314 dorsiflexion angle did not change. Thus, a lower CoM height during the stance phase was
315 observed, which could be explained by the changes in knee and hip flexion angles. Due to the
316 lower and more backward positioning of the CoM, the point of force application under the foot
317 was shifted slightly posteriorly, decreasing the external GRF lever arm of the ankle, but
318 extending the GRF lever arms of the knee and hip joint (Fig. 4). These alterations in GRF lever
319 arms could explain the increases in knee and hip joint torques, as well as the decreases in the
320 ankle joint torque (Fig. 3).

321 *** insert Figure 4 about here ***

322 In this study, we found maximal torque magnitudes to be higher at the ankle joint
323 compared to the more proximal joints during running. In contrast, it has been reported that the
324 maximal voluntary joint torque of the ankle plantar flexors during isolated strength testing is
325 smaller than that of the knee or hip extensors (45). Therefore, our findings could suggest that
326 the ankle plantar flexors might have suffered more from fatigue than proximal muscle groups,
327 probably because the ankle plantar flexors worked closer to their maximal voluntary joint
328 torque capacity compared to knee and hip. Several studies have described decreases in maximal
329 voluntary ankle plantar flexor muscle strength after a 5-km run (36), a half marathon (34), and
330 intensive treadmill running over 2 hours (35). Furthermore, in ultra-marathons, additional
331 fatigue effects in knee and hip extensors have been reported (31–33). Nonetheless, the
332 contraction velocity and joint ankle configuration are different between isometric strength
333 testing and running. Future studies should integrate more sophisticated, non-isometric strength
334 tests utilizing running-specific contraction conditions in order to resolve joint-specific
335 reductions in force generation capacities after fatiguing runs.

336 The finding that maximal ankle torque and positive work decline during a 10-km
337 treadmill run with near-maximal effort seems counterintuitive given the positive characteristics
338 of ankle plantar flexor muscle-tendon unit work for running economy. Our results show that
339 the reduced ankle joint work output was compensated by more positive work at the knee and
340 hip joints, especially for the RR group. This redistribution of positive work towards more
341 proximal muscle groups might lead to a greater metabolic cost. This is because these proximal
342 joint work requirements might be satisfied to a greater extent by work performed by muscle
343 fascicles as compared to tendon energy storage and return. It can be assumed that, in contrast
344 to the knee and hip extensor muscle-tendon units, the TS muscle-tendon unit is better equipped
345 for energy storage and return during running (25,26). Furthermore, shorter muscle fibers reduce

346 the cost of force generation due to a reduction in muscle volume to cross-sectional area ratio
347 (46), which therefore is also assumed to be beneficial for running economy (39). The TS has
348 relatively short fascicles and high pennation angles compared to the knee and hip extensor
349 muscles (37,38). Consequently, force production of the TS might be metabolically less costly
350 compared to long-fibred muscles (25). Accordingly, running economy might be reduced when
351 the TS muscle-tendon unit is less involved in the lower extremity energy exchange, either due
352 to less work performed by tendon energy storage and return or due to higher muscle volume
353 activation at the hip and knee joint. Recent results of Holt and co-workers (47) support the
354 latter explanation. They found that replacing muscle stretch-shortening work with tendon
355 elastic energy storage and return did not significantly reduce the cost of force production.
356 However, due to the limitations of the chosen methodology in the current study, these
357 interpretations are rather speculative and need to be further verified by in vivo assessments of
358 the behavior of lower extremity muscle-tendon units during prolonged fatiguing running.

359 The counter effect of a fatigue induced reduction in TS involvement has been confirmed
360 in a study that demonstrated that an increase in the contractile force of the TS muscle-tendon
361 unit induced by resistance training could improve running economy (3). Furthermore, well-
362 trained distance runners with high running economy typically show greater TS muscle strength
363 and greater tendon-aponeurosis stiffness than runners with lower running economy (4).
364 Previous findings show that running economy substantially reduces when running is performed
365 with an excessively flexed knee joint, also called Groucho running style (6). The observed
366 more flexed knee joint angles (maximal and during touch-down of the foot) in the present study
367 could be a strategy to minimize vertical GRF when running into exhaustion (11). Our findings
368 are furthermore consistent with the work of Peltonen et al. (48) who postulated that changes in
369 running technique result from muscle fatigue. Additionally, Derrick and co-workers (15)
370 assumed that altered kinematics result in increased metabolic costs during the latter stages of

371 an exhausting run. Based on the current findings, the frequently reported increase in oxygen
372 uptake during long-distance running (7,8) may partly be caused by the additional metabolic
373 cost due to the redistribution of work towards more proximal muscle groups potentially because
374 of TS fatigue. For most parameters in the present study we observed a nearly linear change as
375 a function of running distance. Future studies should explore whether this behavior can also be
376 observed for longer running distances or runs with maximal effort or if a rapid alteration in
377 running mechanics occurs at greater levels of fatigue compared to our 10-km treadmill run with
378 near-maximal effort.

379 Due to methodological reasons the present study was performed on a treadmill whereas
380 distance running is most often performed overground. Previous studies have found that
381 differences in lower extremity kinematics between overground and treadmill running are rather
382 small and show inconsistent trends for individual participants, depending on shoe or treadmill
383 condition (49). However, it can be generalized that running on a treadmill leads to a flatter foot
384 strike pattern in comparison to overground running (49,50). This could be partly a protective
385 behavior due to a higher stiffness of force-instrumented treadmills and the associated higher
386 joint loading (51). Furthermore, treadmill running has shown to increase the maximal knee
387 flexion angle and decrease knee extension power with no modifications in ankle plantar flexion
388 power (52). If and to what extent the hard surface of the present treadmill may influence the
389 redistribution in joint kinetics in comparison to overground running, the effect of different
390 cushioning shoes or surfaces like bitumen, Tartan, or forest floor should be investigated in
391 future studies of prolonged fatiguing running. Additionally, an early study suggested that the
392 energy requirements of the runners could be reduced by running on a treadmill because the
393 backward motion of the belt assists the runner by moving the supporting leg back during the
394 stance phase (53). Nonetheless, Riley and co-workers (52) concluded that a treadmill-based

395 analysis of running mechanics can be generalized to overground running mechanics if the belt
396 speed is adequately regulated.

397 When considering our second hypothesis, it is generally accepted that high-
398 performance runners differ from less successful ones mainly in terms of the running economy
399 and fatigability. Therefore, the second hypothesis of the current study was that the RR group
400 would experience a greater running-induced reduction of positive ankle joint work than the CR
401 group. We found a significant ($P < 0.05$) decrease of the positive ankle joint work of the RR
402 group for the first time at 5 km ($P = 0.017$) which continued to decrease up to the end of the
403 run. However, no change of the positive ankle joint work was found for the CR group. Both
404 findings allow us to accept our second hypothesis. The tendency ($p = 0.126$) towards an
405 interaction between performance level and running distance for positive ankle joint work is an
406 additional indication. When trying to explain the greater reduction in the positive ankle joint
407 work of the RR group, we speculate that the RR group suffered more from an ankle plantar
408 flexor muscle fatigue than the CR group. Thus, the CR group showed a tendency towards a
409 lower rate of decrease in positive ankle plantar flexor work. This suggests that the CR group
410 had a higher muscular capacity and attempted to maintain the ankle plantar flexor work as long
411 as possible. Future studies should directly assess the relationship between the redistribution of
412 lower extremity joint work and localized ankle plantar flexor muscle fatigue after prolonged
413 fatiguing runs. Referring to the plantar flexor muscle capacity, an earlier study has shown that
414 well-trained distance runners have greater ankle plantar flexor muscle strength than less trained
415 runners (4) which might indicate a specific adaptation to maintain high positive ankle joint
416 work output in prolonged fatiguing runs. Our results also confirm a significant ($P < 0.001$)
417 group difference for ankle joint torque during running and could be due to the different ankle
418 plantar flexor muscle strength, as well as the dissimilar running velocity. Nevertheless, the
419 running distance main effect for ankle joint torque in our study was significant ($P < 0.001$) and

420 accordingly we found a decrease in ankle joint torque for each group by approximately 5% by
421 the end of the run compared to the beginning. It is noteworthy, however, that the ankle joint
422 torque of both groups was similarly decreased even though there are distinct decreases in the
423 positive ankle joint work.

424 Considering angular velocity could provide a possible explanation for the different
425 reduction of positive ankle joint work between the two groups of runners. We found a
426 significant ($P < 0.016$) interaction between performance level and running distance for ankle
427 plantar flexion velocity. From the beginning to the end of the run, increased ankle plantar
428 flexion velocity (+4%) and knee extension velocity (+7%) were observed in the CR group
429 which might be a compensation strategy to counteract the reduced ankle torque and to maintain
430 the positive ankle joint work generation as long as possible ([see Appendix, SDC 1, Fig. 4 --](#)
431 [Changes in angular velocities](#)~~Fig. 4~~). In contrast to the CR group, we did not find this
432 compensational strategy for the RR group because the ankle plantar flexion velocity did not
433 change when comparing the beginning with the end of the run. Although, during the first 2 km
434 of the run an increase of the ankle plantar flexion velocity (+2%) in the RR group was observed,
435 which could not be maintained until the end of the run ~~(SDC Fig. 4)~~([see Appendix, SDC 1,](#)
436 [Fig. 4 -- Changes in angular velocities](#)). Similar to the CR group, the knee extension velocity
437 was also increased (+6%) over the course of the run in the RR group. Such divergent alteration
438 of angular velocities between the knee extensors and the ankle plantar flexors may be due to
439 fatigued biarticular gastrocnemius muscle-tendon units which usually ensure the mechanical
440 energy transfer between the knee and ankle joint (54,55). Further investigations should
441 examine if the energy transfer between the knee extensors and the foot changes during
442 prolonged fatiguing runs and if this change is due to a reduced capacity of biarticular muscle-
443 tendon units. Based on the data in this study, a discussion of increasing the ankle plantar flexion
444 or knee extension velocity as compensational strategy to maintain positive ankle joint work

445 and the efficiency of energy transfer between knee and ankle remains highly speculative
446 without a detailed analysis of muscles and tendon fascicle behavior through e.g. ultrasound
447 measurements.

448 Despite dissimilar reductions in positive ankle joint work, the ankle joint torque in both
449 groups decreased by approximately 5% by the end of the run compared to the beginning. When
450 considering the minimal changes observed in ankle joint kinematics ($< 2^\circ$ for all parameters)
451 and therefore internal Achilles tendon lever arm, this suggests that less force was acting on the
452 Achilles tendon, leading to a lower strain and hence decreasing energy storage in the tendon.
453 Accordingly, the increase in angular velocity in the CR group must originate from higher
454 muscle fascicle contraction velocity and not by a faster tendon recoil. We did not find a running
455 distance main effect for negative ankle joint work, which suggests that the runners were able
456 to keep the sum of negative muscle fascicle and tendon work relatively constant over the course
457 of the run. It is known that in unfatigued running, both soleus and gastrocnemius medialis
458 muscle fascicles undergo nearly constant shortening during the stance phase by operating from
459 the plateau region towards the ascending limb of muscle force-length relationship (56,57).
460 Therefore, one could speculate that when Achilles tendon strain and therefore energy storage
461 is reduced over the course of the run, the TS muscle fascicles stretch-shortening behavior might
462 have changed as well. More detailed studies should focus on direct measurements of the
463 lengthening and shortening amplitudes of muscle fascicles and tendinous structures when
464 running into exhaustion, potentially with the aid of ultrasonography. These experiments could
465 also consider potential creep effects of tendinous structures, which may attenuate the above
466 described mechanism. Nonetheless, literature reports are contradictory regarding to the
467 possible fatigue-related changes in the material properties through a repeated cyclic loading of
468 the Achilles tendon, e.g. in long-distance running (34,48).

469 **LIMITATIONS**

470 This study has several limitations. First, the individual season best times were self-reported,
471 and it is possible that the participants did not disclose their actual best times. Second, the
472 running economy was not directly quantified. Running economy has consistently been reported
473 to decrease during long-distance runs performed until exhaustion (7,8) and therefore it is very
474 likely that the participants of the present study also suffered from a reduced running economy.
475 In addition, we did not use spirometry because we speculated that wearing the spirometer
476 would affect running mechanics. Third, we did not determine the isometric or isokinetic force
477 capacities of the leg extensors to quantify the possible alteration of muscular capacity before-
478 after the course of the run. And, fourth, we did not directly quantify the viscoelastic behavior
479 of tendinous tissues and the contraction patterns of muscle fascicles of the main leg extensor
480 muscle-tendon units before-after or over the course of the run.

481 **CONCLUSION**

482 Our findings demonstrate that a 10-km treadmill run with near-maximal effort leads to a clear
483 redistribution of joint work from the ankle to the knee and hip joint in recreational runners. The
484 reduction in positive ankle joint work and ankle joint torque may be due to fatigued ankle
485 plantar flexors. This could partly explain the decreased running economy in a prolonged
486 fatiguing run, because the muscle-tendon units crossing proximal joints are less equipped for
487 energy storage and return compared to ankle plantar flexors. Furthermore, due to the activation
488 of the longer muscle fascicles and greater muscle volumes of the more proximal muscle groups
489 can possibly incur a greater metabolic cost. Therefore, in order to improve running
490 performance, long-distance runners may benefit from an exercise-induced enhancement of
491 ankle plantar flexor muscle-tendon unit capacities (TS muscle strength and Achilles tendon
492 stiffness) to postpone the redistribution of work from distal to proximal joints.

493 **ACKNOWLEDGMENTS**

494 The authors thank all participants for their cooperation. We are grateful to Hans-Martin Küsel-
495 Feldker for his engineering help and to Sandra Friedemann, David Joachimmeyer, Marc-David
496 Melchert, Tim Plöger, and Philipp Schäfers for their assistance during the data acquisition and
497 post-processing phases of study.

498 **CONFLICTS OF INTEREST**

499 The manufacturer of the shoes (Adidas AG; Herzogenaurach, Germany) was not involved in
500 the study design or the collection, analysis, or interpretation of data. None of the authors have
501 any financial interests in or affiliations with any organization or entity mentioned in this study.

502 The authors did not receive funding from any organization or company for performing this
503 study. There are no conflicts of interest to declare. The results of the present study are presented
504 clearly, honestly, and without fabrication, falsification, or inappropriate data manipulation. The
505 results of this study do not constitute endorsement by the American College of Sports
506 Medicine.

507 **REFERENCES**

- 508 1. Saunders PU, Pyne DB, Telford RD, Hawley JA. Factors affecting running economy in
509 trained distance runners. *Sports Med.* 2004;34(7):465–85.
- 510 2. Williams KR, Cavanagh PR. Relationship between distance running mechanics,
511 running economy, and performance. *J Appl Physiol.* 1987;63(3):1236–45.
- 512 3. Albracht K, Arampatzis A. Exercise-induced changes in triceps surae tendon stiffness
513 and muscle strength affect running economy in humans. *Eur J Appl Physiol.*
514 2013;113(6):1605–15. doi:10.1007/s00421-012-2585-4
- 515 4. Arampatzis A, Monte G de, Karamanidis K, Morey-Klapsing G, Stafilidis S,
516 Brüggemann G-P. Influence of the muscle-tendon unit's mechanical and morphological
517 properties on running economy. *J Exp Biol.* 2006;209(Pt 17):3345–57.
518 doi:10.1242/jeb.02340

- 519 5. Martin PE, Morgan DW. Biomechanical considerations for economical walking and
520 running. *Med Sci Sports Exerc.* 1992;24(4):467–74.
- 521 6. McMahon TA, Valiant G, Frederick EC. Groucho running. *J Appl Physiol.*
522 1987;62(6):2326–37.
- 523 7. Candau R, Belli A, Millet GY, Georges D, Barbier B, Rouillon JD. Energy cost and
524 running mechanics during a treadmill run to voluntary exhaustion in humans. *Eur J*
525 *Appl Physiol Occup Physiol.* 1998;77(6):479–85.
- 526 8. Kyröläinen H, Pullinen T, Candau R, Avela J, Huttunen P, Komi PV. Effects of
527 marathon running on running economy and kinematics. *Eur J Appl Physiol.*
528 2000;82(4):297–304.
- 529 9. Enoka RM, Duchateau J. Muscle fatigue: what, why and how it influences muscle
530 function. *J Physiol (Lond.)*. 2008;586(1):11–23. doi:10.1113/jphysiol.2007.139477
- 531 10. Girard O, Millet GP, Slawinski J, Racinais S, Micallef JP. Changes in running
532 mechanics and spring-mass behaviour during a 5-km time trial. *Int J Sports Med.*
533 2013;34(9):832–40. doi:10.1055/s-0032-1329958
- 534 11. Rabita G, Slawinski J, Girard O, Bignet F, Hausswirth C. Spring-mass behavior during
535 exhaustive run at constant velocity in elite triathletes. *Med Sci Sports Exerc.*
536 2011;43(4):685–92. doi:10.1249/MSS.0b013e3181fb3793
- 537 12. Morin JB, Samozino P, Millet GY. Changes in running kinematics, kinetics, and
538 spring-mass behavior over a 24-h run. *Med Sci Sports Exerc.* 2011;43(5):829–36.
- 539 13. Hayes PR, Bowen SJ, Davies EJ. The relationships between local muscular endurance
540 and kinematic changes during a run to exhaustion at vVO₂max. *J Strength Cond Res.*
541 2004;18(4):898–903.

- 542 14. Rabita G, Couturier A, Dorel S, Hausswirth C, Le Meur Y. Changes in spring-mass
543 behavior and muscle activity during an exhaustive run at $\dot{V}O_2\text{max}$. *J Biomech*.
544 2013;46(12):2011–7. doi:10.1016/j.jbiomech.2013.06.011
- 545 15. Derrick TR, Dereu D, McLean SP. Impacts and kinematic adjustments during an
546 exhaustive run. *Med Sci Sports Exerc*. 2002;34(6):998–1002.
- 547 16. Koblbauer IF, van Schooten KS, Verhagen EA, van Dieën JH. Kinematic changes
548 during running-induced fatigue and relations with core endurance in novice runners. *J*
549 *Sci Med Sport*. 2014;17(4):419–24. doi:10.1016/j.jsams.2013.05.013
- 550 17. Siler WL, Martin PE. Changes in running pattern during a treadmill run to volitional
551 exhaustion: Fast versus slower runners. *Int J Sport Biomech*. 1991;7(1):12–28.
- 552 18. Dutto DJ, Smith GA. Changes in spring-mass characteristics during treadmill running
553 to exhaustion. *Med Sci Sports Exerc*. 2002;34(8):1324–31.
- 554 19. Hunter I, Smith GA. Preferred and optimal stride frequency, stiffness and economy:
555 Changes with fatigue during a 1-h high-intensity run. *Eur J Appl Physiol*.
556 2007;100(6):653–61. doi:10.1007/s00421-007-0456-1
- 557 20. Arampatzis A, Knicker A, Metzler V, Brüggemann G-P. Mechanical power in running:
558 a comparison of different approaches. *J Biomech*. 2000;33(4):457–63.
- 559 21. Stefanyshyn DJ, Nigg BM. Mechanical energy contribution of the metatarsophalangeal
560 joint to running and sprinting. *J Biomech*. 1997;30(11–12):1081–5.
- 561 22. Belli A, Kyröläinen H, Komi PV. Moment and power of lower limb joints in running.
562 *Int J Sports Med*. 2002;23(2):136–41. doi:10.1055/s-2002-20136
- 563 23. Fukuchi RK, Fukuchi CA, Duarte M. A public dataset of running biomechanics and the
564 effects of running speed on lower extremity kinematics and kinetics. *PeerJ*.
565 2017;5e3298. doi:10.7717/peerj.3298

- 566 24. Roy J-PR, Stefanyshyn DJ. Shoe midsole longitudinal bending stiffness and running
567 economy, joint energy, and EMG. *Med Sci Sports Exerc.* 2006;38(3):562–9.
568 doi:10.1249/01.mss.0000193562.22001.e8
- 569 25. Biewener AA, Roberts TJ. Muscle and tendon contributions to force, work, and elastic
570 energy savings: A comparative perspective. *Exerc Sport Sci Rev.* 2000;28(3):99–107.
- 571 26. Alexander RM. Tendon elasticity and muscle function. *Comp Biochem Physiol, Part A*
572 *Mol Integr Physiol.* 2002;133(4):1001–11.
- 573 27. Kulmala J-P, Korhonen MT, Kuitunen S, et al. Which muscles compromise human
574 locomotor performance with age? *J R Soc Interface.* 2014;11(100):20140858.
575 doi:10.1098/rsif.2014.0858
- 576 28. Paquette MR, Devita P, Williams DSB. Biomechanical implications of training volume
577 and intensity in aging runners. *Med Sci Sports Exerc.* 2018;50(3):510–5.
578 doi:10.1249/MSS.0000000000001452
- 579 29. Devita P, Hortobagyi T. Age causes a redistribution of joint torques and powers during
580 gait. *J Appl Physiol.* 2000;88(5):1804–11. doi:10.1152/jappl.2000.88.5.1804
- 581 30. Devita P, Fellin RE, Seay JF, Ip E, Stavro N, Messier SP. The Relationships between
582 age and running biomechanics. *Med Sci Sports Exerc.* 2016;48(1):98–106.
583 doi:10.1249/MSS.0000000000000744
- 584 31. Saugy J, Place N, Millet GY, Degache F, Schena F, Millet GP. Alterations of
585 neuromuscular function after the world's most challenging mountain ultra-marathon.
586 *PLoS ONE.* 2013;8(6):e65596. doi:10.1371/journal.pone.0065596
- 587 32. Koller A, Sumann G, Schobersberger W, Hoertnagl H, Haid C. Decrease in eccentric
588 hamstring strength in runners in the Tirol Speed Marathon. *Br J Sports Med.*
589 2006;40(10):850–2; discussion 852. doi:10.1136/bjism.2006.028175

- 590 33. Millet GY, Tomazin K, Verges S, et al. Neuromuscular consequences of an extreme
591 mountain ultra-marathon. *PLoS ONE*. 2011;6(2):e17059.
- 592 34. Ackermans TMA, Epro G, McCrum C, et al. Aging and the effects of a half marathon
593 on Achilles tendon force-elongation relationship. *Eur J Appl Physiol*. 2016;116(11–
594 12):2281–92. doi:10.1007/s00421-016-3482-z
- 595 35. Saldanha A, Nordlund Ekblom MM, Thorstensson A. Central fatigue affects plantar
596 flexor strength after prolonged running. *Scand J Med Sci Sports*. 2008;18(3):383–8.
- 597 36. Girard O, Millet GP, Micallef JP, Racinais S. Alteration in neuromuscular function
598 after a 5 km running time trial. *Eur J Appl Physiol*. 2012;112(6):2323–30.
599 doi:10.1007/s00421-011-2205-8
- 600 37. Ward SR, Eng CM, Smallwood LH, Lieber RL. Are current measurements of lower
601 extremity muscle architecture accurate? *Clin Orthop Relat Res*. 2009;467(4):1074–82.
602 doi:10.1007/s11999-008-0594-8
- 603 38. Wickiewicz TL, Roy RR, Powell PL, Edgerton VR. Muscle architecture of the human
604 lower limb. *Clin Orthop Relat Res*. 1983;(179):275–83.
- 605 39. Cavagna GA, Saibene FP, Margaria R. Mechanical work in running. *J Appl Physiol*.
606 1964;19:249–56.
- 607 40. Willwacher S, Kurz M, Menne C, Schrödter E, Brüggemann G-P. Biomechanical
608 response to altered footwear longitudinal bending stiffness in the early acceleration
609 phase of sprinting. *Footwear Science*. 2016;8(2):99–108.
610 doi:10.1080/19424280.2016.1144653
- 611 41. Hof AL. An explicit expression for the moment in multibody systems. *J Biomech*.
612 1992;25(10):1209–11.
- 613 42. Leva P de. Adjustments to Zatsiorsky-Seluyanov's segment inertia parameters. *J*
614 *Biomech*. 1996;29(9):1223–30.

- 615 43. Bell AL, Brand RA, Pedersen DR. Prediction of hip joint centre location from external
616 landmarks. *Hum Mov Sci.* 1989;8(1):3–16. 10.1016/0167-9457(89)90020-1
- 617 44. Cohen J. Statistical power analysis for the behavioral sciences. 2nd ed. Hillsdale, New
618 Jersey: Lawrence Erlbaum Associates Inc; 1988. p. 40, 286–7.
- 619 45. Anderson DE, Madigan ML, Nussbaum MA. Maximum voluntary joint torque as a
620 function of joint angle and angular velocity: Model development and application to the
621 lower limb. *J Biomech.* 2007;40(14):3105–13. doi:10.1016/j.jbiomech.2007.03.022
- 622 46. Roberts TJ, Kram R, Weyand PG, Taylor CR. Energetics of bipedal running. I.
623 Metabolic cost of generating force. *J Exp Biol.* 1998;201(Pt 19):2745–51.
- 624 47. Holt NC, Roberts TJ, Askew GN. The energetic benefits of tendon springs in running:
625 Is the reduction of muscle work important? *J Exp Biol.* 2014;217(Pt 24):4365–71.
626 doi:10.1242/jeb.112813
- 627 48. Peltonen J, Cronin NJ, Stenroth L, Finni T, Avela J. Achilles tendon stiffness is
628 unchanged one hour after a marathon. *J Exp Biol.* 2012;215(Pt 20):3665–71.
629 doi:10.1242/jeb.068874
- 630 49. Nigg BM, De Boer, RW, Fisher V. A kinematic comparison of overground and
631 treadmill running. *Med Sci Sports Exerc.* 1995;27(1):98–105.
- 632 50. Wank V, Frick U, Schmidtbleicher D. Kinematics and electromyography of lower limb
633 muscles in overground and treadmill running. *Int J Sports Med.* 1998;19(7):455–61.
- 634 51. Willy RW, Halsey L, Hayek A, Johnson H, Willson JD. Patellofemoral joint and
635 Achilles tendon loads during overground and treadmill running. *J Orthop Sports Phys
636 Ther.* 2016;46(8):664–72.
- 637 52. Riley PO, Dicharry J, Franz J, Della Croce U, Wilder RP, Kerrigan DC. A kinematics
638 and kinetic comparison of overground and treadmill running. *Med Sci Sports Exerc.*
639 2008;40(6):1093–100. doi:10.1249/MSS.0b013e3181677530

- 640 53. Frishberg, BA. An analysis of overground and treadmill sprinting. *Med Sci Sports*
641 *Exerc.* 1983;15(6):478–85.
- 642 54. Prilutsky BI, Zatsiorsky VM. Tendon action of two-joint muscles: Transfer of
643 mechanical energy between joints during jumping, landing, and running. *J Biomech.*
644 1994;27(1):25–34.
- 645 55. Prilutsky BI, Herzog W, Leonard T. Transfer of mechanical energy between ankle and
646 knee joints by gastrocnemius and plantaris muscles during cat locomotion. *J Biomech.*
647 1996;29(4):391–403.
- 648 56. Rubenson J, Pires NJ, Loi HO, Pinniger GJ, Shannon DG. On the ascent: The soleus
649 operating length is conserved to the ascending limb of the force-length curve across gait
650 mechanics in humans. *J Exp Biol.* 2012;215(Pt 20):3539–51. doi:10.1242/jeb.070466
- 651 57. Lichtwark GA, Bougoulas K, Wilson AM. Muscle fascicle and series elastic element
652 length changes along the length of the human gastrocnemius during walking and
653 running. *J Biomech.* 2007;40(1):157–64. doi:10.1016/j.jbiomech.2005.10.035
- 654

655 **FIGURE LEGENDS**

656 **FIGURE 1:** The individual negative and positive joint work of recreational runners (RR; n =
657 13) and competitive runners (CR; n = 12) at the beginning (0 km) and at the end (10 km) of the
658 10-km treadmill run with near-maximal effort. Significant differences are represented by $*P <$
659 0.05 and $**P < 0.01$. The values in parentheses show the Cohen's d effect sizes.

660

661 **FIGURE 2:** Changes in joint work (means \pm standard deviation) over the course of the 10-km
662 treadmill run with near-maximal effort of recreational runners (RR; n = 13) and competitive
663 runners (CR; n = 12). The gray area represents the standard deviation of the hip joint work. All
664 significant differences from the values at the beginning of the run are represented by $*P < 0.05$
665 and $**P < 0.01$. The values in parentheses show the Cohen's d effect sizes.

666

667 **FIGURE 3:** Changes in external ground-reaction force lever arm of the hip, knee, and ankle
668 joint (means \pm standard deviation) over the course of the 10-km treadmill run with near-
669 maximal effort of recreational runners (RR; n = 13) and competitive runners (CR; n = 12). The
670 gray area represents the standard deviation of the external ground-reaction force lever arm of
671 the knee joint. All significant differences from the values at the beginning of the run are
672 represented by $*P < 0.05$. The values in parentheses show the Cohen's d effect sizes.

673

674 **FIGURE 4:** Schematic illustration of the stance phase during maximal vertical ground-reaction
675 force (GRF_{vert}) at the beginning (0 km, unfilled lines) and the end (10 km, black lines) of the
676 10-km treadmill run with near-maximal effort. GRF_{vert} , joint angles and segment lengths are
677 not to scale, as also the dashed lines representing external ground-reaction force lever arm of
678 the hip, knee, and ankle joint. The percentage rates at each joint represent the relative changes
679 of positive joint work after the 10-km treadmill run of recreational (RR; top value) and

680 competitive (CR; bottom value) runners. **Note:** The 10-km treadmill run with near-maximal
681 effort led to increased knee and hip joint torques as well as a decreased ankle joint torque,
682 probably due to fatigue of the ankle plantar flexors. The flexion angle of knee and hip joints
683 increased slightly, but there were no alterations in the ankle joint angle. Hence, the center of
684 mass (CoM_{min}) shifted slightly deeper and posteriorly, causing the point of force application
685 under the foot to shift, thereby modifying the external ground-reaction force lever arms
686 (decrease at ankle joint and increase at knee and hip joints). The positive joint work
687 contribution shifted from the ankle joint to proximal joints.

688

689 **TABLE 1:** Positive (pos) and negative (neg) total joint works, maximal (max) external joint
690 torques, and external lever arms at maximal vertical ground-reaction force (GRF_{max}) of lower
691 extremity joints (mean \pm standard deviation) for recreational runners (RR; $n = 13$) and
692 competitive runners (CR; $n = 12$) at the beginning (0 km) and at the end (10 km) of the 10-km
693 treadmill run with near-maximal effort. **Note:** Significant differences between 0 km and 10 km
694 are represented by $**P < 0.01$. The values in parentheses show the Cohen's d effect sizes. To
695 explain the group difference between RR and CR, the partial eta squared (η_p^2) values are
696 presented, as well as the running distance main effect and interaction effect between
697 performance level and running distance.

698

699 **TABLE 2:** Kinematic parameters of lower extremity joints (mean \pm standard deviation) for
700 recreational runners (RR; $n = 13$) and competitive runners (CR; $n = 12$) at the beginning (0 km)
701 and the end (10 km) of the 10-km treadmill run with near-maximal effort during foot touch-
702 down (TD), maximal values (max), maximal vertical ground-reaction force (GRF_{max}), and toe-
703 off (TO). The center of mass (CoM) height at foot touch-down (CoM_{TD}), and the minimal
704 height (CoM_{min}) during the stance phase. **Note:** Significant differences between 0 km and 10

705 km are represented by $*P < 0.05$ and $**P < 0.01$. The values in parentheses show the Cohen's
706 d effect sizes. To explain the group difference between RR and CR, the partial eta squared (η_p^2)
707 values are presented, as well as the running distance main effect and interaction effect between
708 performance level and running distance.

709

710 **SUPPLEMENTAL DIGITAL CONTENT**

711 SANN0_SDC_Positive_work_contribution_R2.pdf

712